


Allocation trade-offs impact organ size and muscle architecture in an invasive population of *Xenopus laevis* in Western France

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Abstract

Invasive species are a global scourge and often negatively impact native species. Understanding the expansion and dispersal limits of these species is essential. As previous studies have demonstrated increased locomotor performance for populations at the edge of the range of expanding populations, studies of locomotion including the anatomical and physiological traits underlying dispersal capacity are of interest. We focus here on an invasive population of *Xenopus laevis* introduced in France nearly forty years ago. Previous studies have demonstrated differences in mobility between populations from the centre and the edge of the invasive range, with individuals from the range edge possessing a higher endurance capacity. We test here whether range-edge frogs show anatomical differences in organs or muscles underlying these observed differences of performance. We dissected 10 males and 10 females from central and range-edge sites (40 animals in total) and measured the mass of their organs and the mass, the length, and the physiological cross-sectional area (PCSA) of 28 hind limb muscles. Our results show anatomical differences with individuals from the range edge possessing heavier, longer and more forceful muscles. Moreover, females from the range edge had a heavier heart but lighter stomach than those of the centre of the range. Future studies comparing the morphology between native and invasive populations in other regions or for other species will be especially insightful to better understand the possible adaptive changes in invasive populations and the limits on dispersal capacity.

Key words: anatomy; dispersal; frog; invasive species; locomotion; trade-offs.

Introduction

Invasive species are often introduced by human activities and can pose a significant threat for biodiversity (Alford & Richards, 1999; Gibbons et al. 2000; Clavero & García-Berthou, 2005). Invaders often have dispersal traits that allow them to spread quickly, rapidly invading new ecosystems and often negatively affecting local species. Locomotion is a mechanical action defined by cycles of muscle contraction made possible by the metabolic energy produced. The architecture of a muscle is critical, as it determines its ability to produce and maintain power (Fukunaga et al. 1992; Burkholder et al. 1994). Blood flow rates and oxygen transfer also play a major role in locomotion (especially for endurance capacity) and their efficiency is directly affected by the cardiovascular system (i.e. the size of the heart and lungs; Farrell et al. 1990;

Young et al. 2002). Moreover, energy supply to the muscles is limited by the digestive system, whose size is related to the maximal rate of energy assimilation (Weiner, 1992). Active dispersal through locomotion is thus determined by central organs (heart, lungs, digestive system), which provide energy and oxygen to the musculoskeletal system. Furthermore, allocation trade-offs (Van Noordwijk & de Jong, 1986; Stearns, 1989) may come into play. If more resources are invested into dispersal, this may come at a cost to other traits such as reproductive output (Mole & Zera, 1993; Veasey et al. 2001; Hughes et al. 2003; Courant et al. 2017). Understanding these trade-offs and how they can lead to an increase in dispersal capacity is therefore crucial in the management of invasive species.

Xenopus laevis is an anuran native from sub-Saharan Africa that has become invasive on a global scale (Tinsley et al. 2009). This species impacts local fauna (Lafferty & Page, 1997; Lobos & Jaksic, 2005; Eggert & Fouquet, 2006; Robert et al. 2007; Lillo et al. 2011; Courant et al. 2018a, 2018b) and their range has been suggested to likely increase under different climate change scenarios (Ihlow et al. 2016), making them of prime concern. *Xenopus laevis* was introduced in the department of Deux-Sèvres, France,

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in the late 1980s (Fouquet, 2001). Their range has been increasing ever since and encompasses more than 207 km² (Measey et al. 2012), with a dispersal rate estimated at 0.5–2 km a year (Grosset et al. 2006). Previous studies have shown that individuals at the dispersal front show a higher *in vivo* endurance capacity and a lower standard metabolic rate (SMR) than individuals from populations near the centre of the range (Louppe et al. 2017, 2018). Moreover, animals at the dispersal front show a lower investment in reproduction compared with animals from the centre of the range (Courant et al. 2017). However, the anatomical traits underlying the differences in locomotor performance and dispersal capacity remain poorly understood.

Leg length has been shown to be responsible for 77% of the inter-individual variation in absolute maximal jump distance in *Pelophylax* kl. *esculentus* (Tejedo et al. 2000), suggesting that overall limb dimensions may be one of the principal drivers of dispersal capacity. On the other hand, James et al. (2005) found that a combination of the mass of the gastrocnemius, the total mass of the hind limb muscles, and pyruvate-kinase activity together explain 62% of the inter-individual variation in maximum jump distance in *Hypsiboas bischoffi*. This suggests that, in addition to variation in overall limb length variation, muscle mass and muscle contractile properties may also drive variation in dispersal capacity. *Xenopus laevis* relies mainly on aquatic locomotion but has been observed to migrate overland with maximum direct observed dispersal distances of up to 2 km (Measey, 2016). Consequently, differences in dispersal capacity between individuals from the centre and the front of the range should be reflected in traits that enhance dispersal capacity. Hind limb length has previously been demonstrated to be greater, for example, in animals from the range edge (Louppe et al. 2017). However, whether other anatomical differences exist remains to be tested.

Here, we compare the architecture of hind limb muscles and the mass of the major organs between individuals of *X. laevis* from the centre and the periphery of the range in France. As dispersal-promoting traits should be selected for in range-edge individuals (Chuang & Peterson, 2016), we predict differences in the force-generating capacity of the limb muscles for range-edge frogs. Moreover, we predict that organs involved in promoting sustained activity such as lungs or heart would be larger in animals from the range edge. Finally, we predict relatively larger muscles in males than females, given the known differences in size-corrected performance between males and females in *Xenopus* frogs (Herrel et al. 2012).

Materials and methods

Animals and dissections

Xenopus laevis ($n = 40$) were sampled in April 2016 in the department of Deux-Sèvres, France, euthanised as required by French law, fixed in formaldehyde, and stored in a 70% aqueous ethanol solution

in the laboratory of Comparative Anatomy of the National Museum of Natural History in Paris, France. Forty animals were dissected, 10 males and 10 females from the centre of the range and 10 males and 10 females from the periphery of the range. Animals were dissected and organs were removed from the abdomen including the heart, the liver, the stomach, the lungs and the kidneys. Next we isolated 28 hind limb muscles: coccygeosacralis, coccygeoiliacus, iliacus externus, iliacus internus, tensor fascia latae, sartorius, gluteus maximus, cruralis, semitendinosus, semimembranosus, gracilis major, gracilis minor, iliofemoralis, iliofibularis, adductor magnus, adductor longus, gemellus, pectineus, obturator internus, obturator externus, quadratus femoris, peroneus, tibialis anticus, tibialis posticus, gastrocnemius, extensor cruris, flexor tarsi anterior, flexor tarsi posterior. Muscles were identified and named following the nomenclature of Gaupp (1896). Muscles were stored in tubes filled with 70% ethanol.

Measurements

After removal of the excess ethanol, organs and muscles were weighed using an electronic balance (Mettler AE100; 109 g/0.1 mg). Muscle connective tissue was dissolved by placing the muscles in a petri dish with a 30% aqueous nitric acid (HNO₃ 30%) solution for 24–48 h. Afterwards, the nitric acid solution was removed and replaced with 50% aqueous glycerol (C₃H₈O₃) to arrest the acid digestion. Muscle fibres were teased apart and placed on a black background with a scale. Twenty fibres were photographed for each muscle and measured using IMAGEJ 1.50i (Wayne Rasband, National Institutes of Health, USA). The mean fibre length was then calculated and used in our estimation of physiological cross-sectional area (PCSA).

$$PCSA = \frac{\text{mass (g)}}{\text{muscular density (g.cm}^{-3}) * \text{fibre length (cm)}}$$

A muscular density of 1.06 g.cm⁻³ (Mendez & Keys, 1960) was used.

As some muscles (nine of 1120) reacted badly to nitric acid digestion, we were unable to obtain measurements of their fibre length. As fibre length scaled with snout-vent length for all muscles, we used a linear regressions of fibre length on snout-vent length (svl) to estimate the fibre lengths for these nine muscles.

Following previous authors (Calow & Alexander, 1973; Kargo & Rome, 2002; Prikryl et al. 2009) and our dissections we grouped our 28 muscle variables into 10 functional groups (Fig. 1): femur protractor (iliacus externus, iliacus internus, iliofemoralis), femur retractors (gemellus, obturator externus, semimembranosus, gracilis major, gracilis minor, iliofibularis), knee extensors (tensor fascia latae, cruralis, gluteus maximus, extensor cruris), ankle extensors (gastrocnemius, tibialis posticus), knee flexors (iliofibularis, semitendinosus), ankle flexors (tibialis anticus, peroneus, flexor tarsi anterior, flexor tarsi posterior), femur adductors (adductor magnus, adductor longus, sartorius), gliding of the ilium along the sacrum (coccygeoiliacus), rotation of the femur (obturator internus), and stabilisers (ilium-urostyle: coccygeosacralis; hip: pectineus, quadratus femoris). The mass and the PCSA of each muscle in a group were added to calculate the summed mass and PCSA. The mean fibre length from all muscles in a group was also calculated (Table 1).

Statistical analyses

Each measurement was log₁₀-transformed before analyses to fulfil the assumptions of normality and homoscedasticity. The

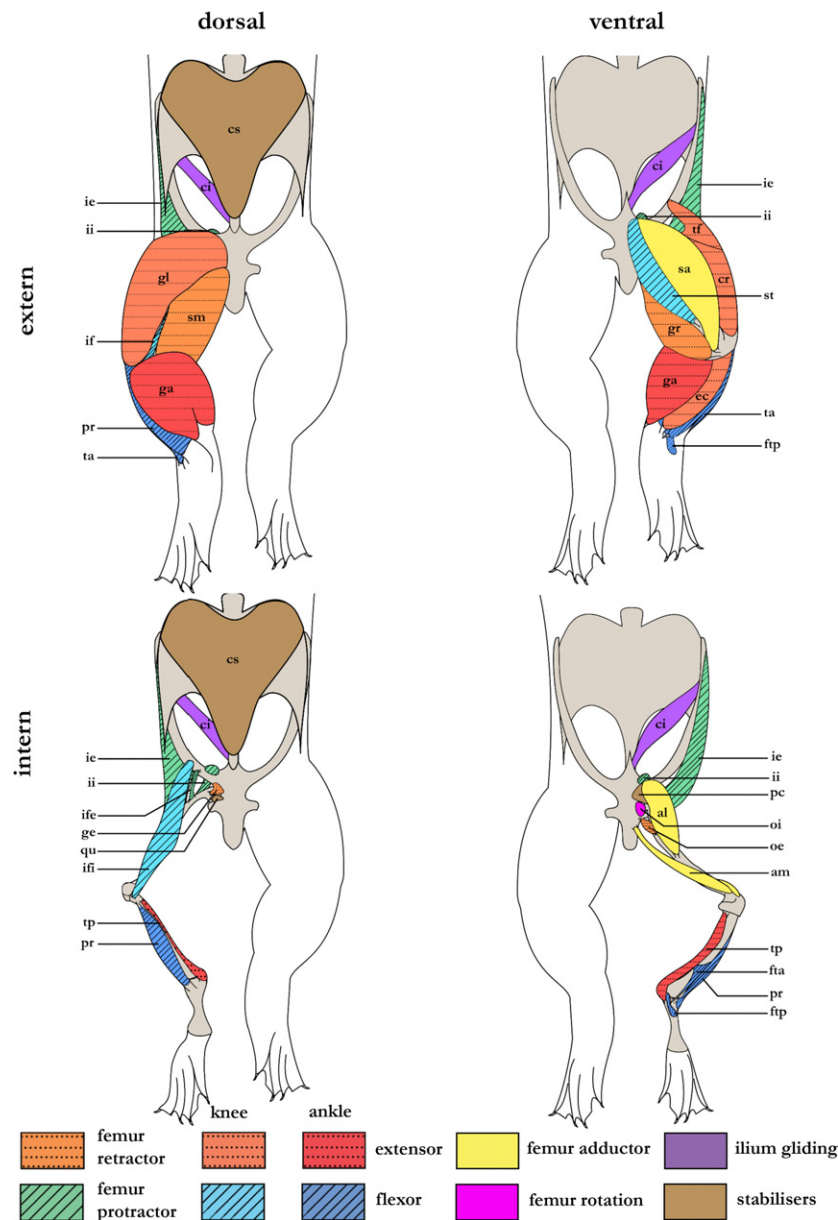


Fig. 1 Schematic drawing of the 28 hind limb muscles dissected. Colours represent functional groups. al, adductor longus; am, adductor magnus; ci, coccygeiliacus; cr, cruralis; cs, coccygeosacralis; ec, extensor cruris; fta, flexor tarsi anterior; ftp, flexor tarsi posterior; ga, gastrocnemius; ge, gemellus; gm, gluteus maximus; gr, gracilis major and minor; ie, iliacus externus; if, iliofemoralis; ifi, iliofibularis; ii, iliacus internus; oe, obturator externus; oi, obturator internus; pc, pectineus; pr, peroneus; qu, quadratus femoris; sa, sartorius; sm, semimembranosus; st, semitendinosus; ta, tibialis anterior; tf, tensor fascia latae; tp, tibialis posterior.

significance threshold was set at $\alpha = 0.05$. All analyses were performed using SPSS V.23 (SPSS Inc., Chicago, IL, USA). Multivariate analyses of covariance (MANCOVA) coupled to univariate analyses of covariance were performed on the \log_{10} -transformed organ masses with \log_{10} -transformed snout-vent length as a covariate to test for differences between centre and edge individuals and between the two sexes. Next, three different MANCOVAs coupled to univariate analyses of covariance were performed on the \log_{10} -transformed mass, length and PCSA data for the different functional groups, with sex and locality as fixed factors and the \log_{10} -transformed snout-vent length as a covariate.

Results

Organ mass

The MANCOVA detected significant effects of SVL ($F_{3,10} = 29.6$, $P < 0.001$), sex ($F_{3,10} = 3.39$, $P = 0.015$) and locality ($F_{3,10} = 8.73$, $P < 0.001$) but no interaction between sex and locality ($F_{3,10} = 1.57$, $P = 0.19$). Given the significant sex effect we then tested for an effect of locality for each sex separately. For females, the heart and the stomach differed

between the two localities (heart: $F_{1,10} = 6.1$, $P = 0.02$; stomach: $F_{1,10} = 4.81$, $P = 0.04$), with individuals from the periphery having a larger heart and individuals from the centre having a larger stomach (Fig. 2). Males showed significant differences in the mass of the liver ($F_{1,10} = 6.61$, $P = 0.02$), with individuals from the centre having a larger liver (Fig. 2).

Muscle architecture

The MANCOVA on the mass of the functional groups showed a significant effect of SVL ($F_{3,10} = 35$, $P < 0.001$) sex ($F_{3,10} = 2.4$, $P = 0.03$) and locality ($F_{3,10} = 2.8$, $P = 0.01$). The

interaction between sex and locality was not significant (interaction: $F_{3,10} = 0.36$, $P = 0.95$). Tests of between subject effects showed that locality had a significant effect on femur retractors ($F_{1,20} = 12$, $P < 0.01$), both extensor groups (knee extensors: $F_{1,20} = 7$, $P < 0.01$; ankle extensors: $F_{1,20} = 11$, $P < 0.01$), and the ankle flexors ($F_{1,20} = 8.2$, $P < 0.01$). Individuals from the periphery had heavier muscles than the ones from the centre (Fig. 3A). The sex effect was significant for femur retractors ($F_{1,20} = 4.6$, $P = 0.04$), knee and ankle extensors, knee and ankle flexors (knee extensors: $F_{1,20} = 9.4$, $P < 0.01$; ankle extensors: $F_{1,20} = 14$, $P < 0.01$; knee flexors: $F_{1,20} = 4.3$, $P = 0.04$; ankle flexors: $F_{1,20} = 7.6$, $P < 0.01$) and femur adductors ($F_{1,20} = 7.7$,

Table 1 Raw mean values \pm standard deviations of the mass, length, and PCSA of each functional muscle groups in *Xenopus laevis*.

	n	fpro mass (g)	fretra mass (g)	ke mass (g)	ae mass (g)	kf mass (g)	af mass (g)	fadd mass (g)	frot mass (g)	iglid mass (g)	stab mass (g)
Centre	20	0.90 \pm 0.4	0.62 \pm 0.29	1.32 \pm 0.58	1.16 \pm 0.52	0.63 \pm 0.25	0.49 \pm 0.2	0.82 \pm 0.36	0.014 \pm 0.014	0.21 \pm 0.12	0.18 \pm 0.09
Periphery	20	0.89 \pm 0.46	0.63 \pm 0.25	1.3 \pm 0.6	1.19 \pm 0.61	0.59 \pm 0.28	0.5 \pm 0.23	0.78 \pm 0.34	0.010 \pm 0.006	0.18 \pm 0.08	0.17 \pm 0.07
	n	fpro length (cm)	fretra length (cm)	ke length (cm)	ae length (cm)	kf length (cm)	af length (cm)	fadd length (cm)	frot length (cm)	iglid length (cm)	stab length (cm)
Centre	20	1.54 \pm 0.31	1.11 \pm 0.18	1.27 \pm 0.14	1.04 \pm 0.11	1.13 \pm 0.21	1.22 \pm 0.15	1.58 \pm 0.29	0.33 \pm 0.07	1.83 \pm 0.33	0.38 \pm 0.08
Periphery	20	1.54 \pm 0.32	1.19 \pm 0.15	1.28 \pm 0.17	1.05 \pm 0.16	1.21 \pm 0.25	1.29 \pm 0.15	1.65 \pm 0.23	0.32 \pm 0.10	2.15 \pm 0.35	0.41 \pm 0.08
	n	fpro PCSA (cm ²)	fretra PCSA (cm ²)	ke PCSA (cm ²)	ae PCSA (cm ²)	kf PCSA (cm ²)	af PCSA (cm ²)	fadd PCSA (cm ²)	frot PCSA (cm ²)	iglid PCSA (cm ²)	stab PCSA (cm ²)
Centre	20	0.38 \pm 0.11	0.43 \pm 0.16	0.86 \pm 0.32	0.76 \pm 0.31	0.5 \pm 0.14	0.34 \pm 0.09	0.43 \pm 0.12	0.04 \pm 0.04	0.10 \pm 0.04	0.82 \pm 0.34
Periphery	20	0.39 \pm 0.15	0.41 \pm 0.13	0.85 \pm 0.31	0.76 \pm 0.27	0.44 \pm 0.17	0.34 \pm 0.13	0.39 \pm 0.12	0.03 \pm 0.02	0.08 \pm 0.03	0.70 \pm 0.24

ae, ankle extension; af, ankle flexion; fadd, femur adductor; fpro, femur protractor; fretra, femur retractor; frot, femur rotation; iglid, ilium gliding; ke, knee extension; kf, knee flexion; stab, stabilisers.

Note that svl was not taken into account.

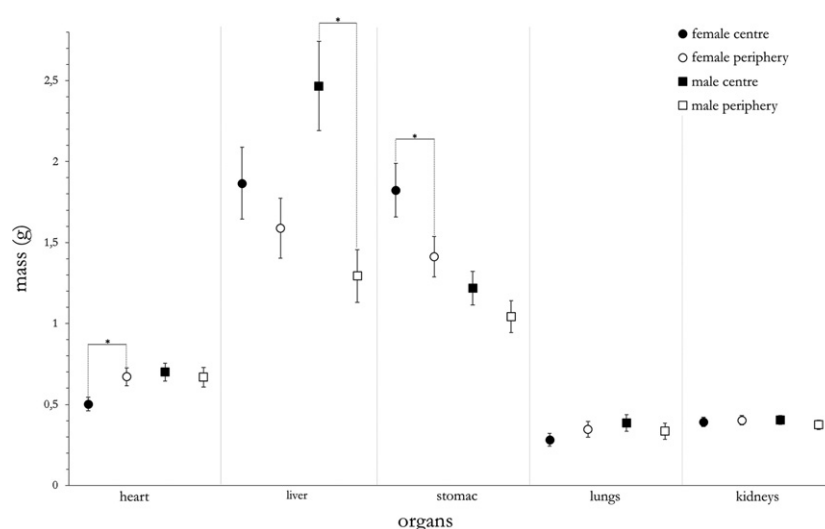


Fig. 2 Organ mass corrected by snout-vent length for two populations and each sex. Symbols represent means \pm standard errors. Circles represent females and squares, males. Filled symbols represent animals from the centre of the invasive range, open symbols depict the animals from the periphery. An asterisk linking two data points highlights statistically significant differences ($P < 0.05$).

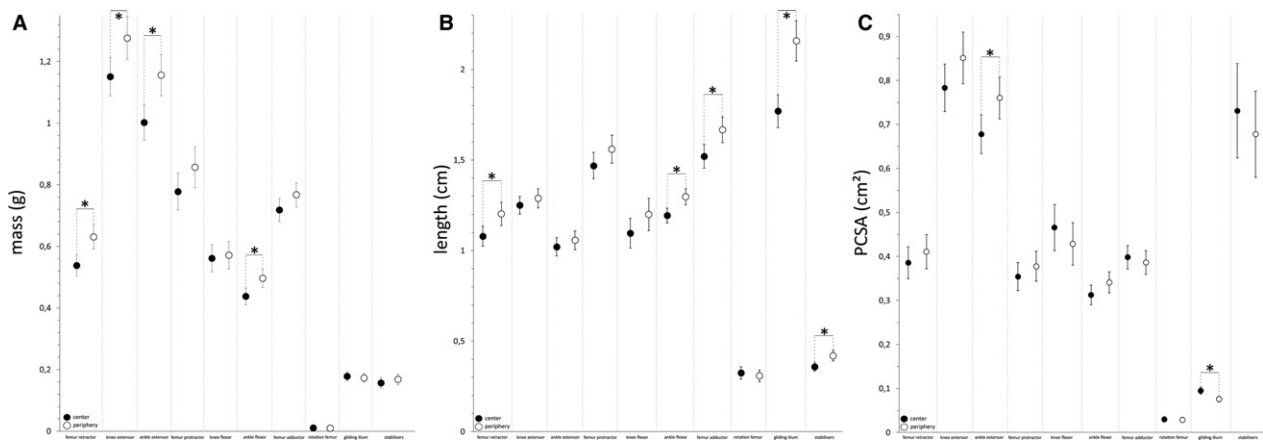


Fig. 3 (A) Summed mass of the 10 functional groups corrected by snout-vent length for the two populations. (B) Average fibre length of the 10 functional groups corrected by snout-vent length for the two populations. (C) Summed PCSA of the 10 functional groups corrected by snout-vent length for the two populations. Symbols represent means \pm standard errors. Filled symbols represent animals from the centre of the invasive range, open symbols animals from the periphery. An asterisk linking two data points highlights statistically significant differences ($P < 0.05$).

$P < 0.01$). In each case, males had heavier muscles than females for a given size.

The MANCOVA on the average fibre length was only significant for SVL and locality (SVL: $F_{3,10} = 14$, $P < 0.001$; sex: $F_{3,10} = 1.4$, $P = 0.20$; locality: $F_{3,10} = 4.9$, $P < 0.01$; interaction: $F_{3,10} = 1.6$, $P = 0.15$). Locality showed an effect on the fibre length of the femur retractors ($F_{1,20} = 7.9$, $P < 0.01$), the ankle flexors ($F_{1,20} = 10$, $P < 0.01$), the femur adductors ($F_{1,20} = 8.9$, $P < 0.01$), the muscle responsible for the gliding of the ilium along the sacrum ($F_{1,20} = 28$, $P < 0.001$), and the stabiliser group ($F_{1,20} = 9.6$, $P < 0.01$), with individuals from the periphery having longer muscle fibres compared with the individuals from the centre (Fig. 3B). Only the femur protractors group showed a significant sex effect ($F_{1,20} = 6$, $P = 0.02$), with males having longer muscle fibres in the protractors compared with females.

The MANCOVA performed on summed PCSA of the functional groups showed significant effects of SVL and locality (SVL: $F_{3,10} = 18$, $P < 0.001$; sex: $F_{3,10} = 1.4$, $P = 0.2$; locality: $F_{3,10} = 3.9$, $P < 0.01$; interaction: $F_{3,10} = 1$, $P = 0.4$). Differences were significant for the ankle extensors ($F_{1,20} = 6.4$, $P = 0.016$) and the muscle responsible for the gliding of the ilium along the sacrum ($F_{1,20} = 13.9$, $P < 0.01$), with individuals from the periphery having more forceful ankle extensors but a less forceful muscle driving the gliding of the pelvis (Fig. 3C). Only the ankle extensors showed a significant sex effect ($F_{1,20} = 5$, $P = 0.03$), with males having a higher PCSA of the ankle extensors compared with females.

Discussion

Differential investment in organ mass

Females from the periphery have a significantly larger heart than do females from the centre of the range. This

result is in accordance with our *a priori* hypothesis suggesting that traits important for locomotor performance, and especially endurance, should be more developed in individuals from the range edge. Indeed, in humans, endurance training is known to cause a hypertrophy of the heart with an increase specifically in the left ventricular mass and volume (see George et al. 2012). In contrast, in males no differences in heart mass were observed between individuals from the centre and the periphery of the range. Unexpectedly, males have a heart that is similar in size to that of females from the periphery despite their smaller overall size. In general, male *X. laevis* have a more nomadic behaviour and move more than females irrespective of the population (Courant, 2017), possibly because males actively engage in mate-searching, whereas females remain more sedentary. Females on the range edge, however, show higher endurance and move more than females from the centre (Courant, 2017), imposing constraints on endurance capacity and thus possibly also heart mass. Females from the centre of the range also have larger stomachs, and males a larger liver, than females and males from the periphery. The stomach and liver have multiple functions, primarily linked to digestion; however, the liver especially also plays a role in storing and producing energy and in detoxification. Although these functions are likely critical to all individuals, the reduced size of these organs in individuals of the periphery of the range may be a reflection of an energetic trade-off where animals from the periphery do not have enough resources to invest in both locomotor-related traits and other organs. This is in accordance with the results of an earlier study that demonstrated allocation trade-offs in *X. laevis* from France, with animals on the range edge investing less in reproduction than those at the centre of the range (Courant et al. 2017).

Muscle architecture

For each type of measurement (mass, length, PCSA), individuals of the range edge had higher mean values, suggesting that they have heavier muscles with longer fibres, but also a greater physiological cross-sectional area (Fig. 3A–C). Previous studies (Louppe et al. 2017, 2018) have shown that individuals from the periphery have a greater stamina and a lower standard metabolic rate (SMR) for their body size. Larger muscles with longer fibres should result in greater power output and faster contractile velocity, traits that likely enhance jumping performance (James et al. 2007). However, whether frogs from the periphery of the range show enhanced jumping burst performance remains to be tested. Given the known trade-off between endurance and burst performance in the closely related species *X. tropicalis* (Herrel & Bonneaud, 2012b), this may not be the case. Future studies investigating the contractile physiology of the limb muscles in animals from the centre and the periphery of the range will be important to better understand how the observed differences in muscle architecture may result in greater endurance capacity in range-edge frogs.

Interestingly, the ankle extensor group was one of the two functional groups to show differences in force generating capacity (PCSA) between the two localities (Fig. 3C). This functional group is composed of the gastrocnemius and the tibialis posticus, muscles known to be important during swimming and jumping (Richards & Biewener, 2007). Our findings suggest that animals on the range edge, in addition to showing more overland movements and having greater endurance capacity may also swim more. If so, the range expansion by following aquatic water courses may be a neglected dispersal strategy in these frogs. Future studies examining differences in swimming speed and endurance between individuals from the centre and from the periphery of the range would be needed to test this idea. The coccygeoiliacus muscle was the only muscle to show opposite results, with individuals from the centre showing larger muscles (Fig. 3C). The sliding of the pelvis caused by the contraction of the coccygeoiliacus muscle was suggested as an anti-predator adaptation when animals are breathing at the surface of the water (Videler & Jorna, 1985). Our results suggest that the individuals from the centre may contract their body more quickly if they have to escape a predator when breathing at the surface of water. Studies involving high-speed recordings of escape behaviour could be performed to test this idea. In addition to the observed differences between centre and periphery, some differences were observed between the sexes, with males typically having larger and more forceful muscles. Previous studies have shown that size-corrected limb dimensions were greater for males than females in *X. laevis* (Louppe et al. 2017) or *X. tropicalis* (Herrel et al. 2012). Our muscle architecture results corroborate the sex differences in these morphological traits, which may explain the greater size-corrected locomotor performance in males than females.

Although we have demonstrated significant differences in organ mass and muscle architecture between populations, the selective mechanisms underlying these differences remain poorly understood. Different processes such as natural selection, 'spatial sorting' (Shine et al. 2011), plasticity or epigenetic factors could all underlie the observed changes. Additional work is clearly needed to identify the role that these processes may play in driving the observed divergence in range-edge frogs. Moreover, multiple environmental factors may have an impact on amphibians when they reach the adult stage (Álvarez & Nicieza, 2002; Měráková & Gvoždík, 2009). Previous studies highlighted that temperature, quantity of food, predation and desiccation during development may all have an effect on growth and hind limb size (Gomez-Mestre et al. 2010; Tejedo et al. 2010). Knowing that hind limb length strongly impacts exertion capacity, swimming speed and jump force (Herrel & Bonneaud, 2012a, 2012b; Herrel et al. 2012, 2014; Louppe et al. 2017) and understanding how environmental factors impact muscle development appears critical.

In summary, we demonstrated anatomical differences in range-edge vs. range-centre individuals of invasive French *X. laevis*. Our results show greater allocation to organs and muscles important to locomotion at the range edge. In contrast, animals from the centre of the range appear to invest more in the digestive system, possibly reflecting an allocation trade-off. Future studies investigating the physiology of the locomotor muscles will be particularly insightful in linking the observed differences in muscle architecture to whole-organism endurance capacity.

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